BioSystems 138 (2015) 18–24

Contents lists available at ScienceDirect

BioSystems

journal homepage: www.elsevier.com/locate/biosystems

Chaos control via feeding switching in an omnivory system

Joydev Chattopadhyay[a,*], Nikhil Pal[b], Sudip Samanta[a], Ezio Venturino[c], Q.J.A. Khan[d]

[a] Agricultural and Ecological Research Unit, Indian Statistical Institute, 203, B. T. Road, Kolkata 700108, India
[b] Department of Mathematics, Visva-Bharati University, Santiniketan 731235, India
[c] Dipartimento di Matematica "Giuseppe Peano", Università di Torino, via Carlo Alberto 10, 10123 Torino, Italy
[d] Department of Mathematics and Statistics, College of Science, Sultan Qaboos University, P.O. Box 36 Al-Khod, Postal Code 123, Oman

ARTICLE INFO

Article history:
Received 9 December 2014
Received in revised form 14 October 2015
Accepted 25 October 2015
Available online 29 October 2015

Keywords:
Three-species Lotka–Volterra model
Predator switching
Omnivory
Chaos
Stability

ABSTRACT

Tanabe and Namba (*Ecology*, **86**, 3411–3414) studied a three species Lotka–Volterra model with omnivory and explored that omnivory can create chaos. It is well documented that predator switching is a similar biological phenomenon to omnivory and likely to occur simultaneously. In the present paper, the tri-trophic Lotka–Volterra food web model with omnivory and predator switching is re-investigated. We observe that if we incorporate predator switching in the system and the intensity of predator switching increases above a threshold value, then the system will be stable from chaotic dynamics. To study the global dynamics of the system extensive numerical simulations are performed. Our analytical and numerical results suggest that predator switching mechanism enhances the stability and the persistence of a food chain system.

1. Introduction

An interesting and appealing topic in population ecology is the understanding of the diversity and community composition of the populations which ultimately determine the overall stability of an ecosystem. The predators have in general a rigid type of feeding pattern, which may be the choice of a specific prey, or it may be dependent on the abundance of the prey. In this latter case looking for resources, the predator moves toward another prey, which may be present in the same or in another habitat. This mechanism of preferential predation is named switching, (Tansky, 1978). Many examples of predator feeding switching have been identified in nature, (Fisher-Piette, 1934; Murdoch, 1969), as well as in laboratory experiments involving *Notonecta* and *Ischnura*, (Lawton et al., 1974). Several mathematical models have been proposed with predator switching involving one predator with two prey species (Holling, 1961; Khan et al., 2004, 1998; Holgate, 1989; Teramoto et al., 1979; Vilcarromero et al., 1979). Extensions to the case in which a predator together with healthy and diseased prey are considered in place of a food chain can be found in (Hotopp et al., 2009, 2010). Recently, we have investigated the effect of omnivory and predator switching in a tri-trophic food chain model with Holling type-II functional responses (Pal et al., 2014). We theoretically explored that if the top predator switch it's feeding between middle predator and basal prey, then predator switching can stabilize an otherwise chaotic system.

In an omnivory food web, a predator consumes more than one prey species. In particular, in a tri-trophic food chain with omnivory, top predator predates both the bottom prey and the intermediate predator (Pimm and Lawton, 1978). This phenomenon is also termed intraguild predation (IGP), defined as the feeding of the intermediate predator by a top predator that can also consume the prey of the intermediate predator (Polis et al., 1989). Thus, the top predator and the intermediate predator species are also potentially competitors for the common resource, i.e. the prey at the lowest trophic level. This fact enhances the chance of switching feeding behavior of the top predator between the bottom prey and the intermediate predator.

Whether omnivory phenomena act as a stabilizing or destabilizing factor in a dynamical population system is still debated, see (Kimbrell and Holt, 2004) and the references therein. A stabilizing effect is found, for instance, in Ref. (Ajraldi and Venturino, 2008; Kooi and Kooijman, 2000). Omnivory with nonlinear functional responses had been investigated showing that omnivory could be a stabilizing factor (McCann and Hastings, 1997). On the other hand, omnivory could destabilize a three species Lotka–Volterra model with linear functional responses, see (Holt and Polis, 1997).

* Corresponding author.
E-mail addresses: joydev@isical.ac.in (J. Chattopadhyay), ezio.venturino@unito.it (E. Venturino).

http://dx.doi.org/10.1016/j.biosystems.2015.10.006
0303-2647/

Furthermore, the Lotka–Volterra model with omnivory could exhibit a limit cycle and coexistence of all species in the omnivory system is possible if the intermediate predator is superior at exploitative competition for the prey, whereas the top predator gains significantly from its consumption of intermediate predator (Holt, 1997). Furthermore, the top predator may become extinct if the predation rate and the conversion efficiency from the prey to predator are very low, whereas the intermediate predator will disappear if the predation rate and the conversion efficiency from prey to predator are high enough. Also recently, in the very same model, chaotic behavior has been numerically discovered, (Tanabe and Namba, 2005).

Recently, we have re-investigated the Hastings and Powell model (Hastings and Powell, 1991) by considering omnivory and predator switching into the model system. We studied step by step the impact of omnivory and predator switching on the dynamics of the system. We have observed that if the consumption rate of top predator on basal prey is increased, then the system will be stable and above a threshold value of the consumption rate (omnivory) the middle predator will be extinct from the system as the middle predator faces food scarcity as well as predation pressure simultaneously. Further, we observed that if the top predator switches it is feeding between middle predator and basal prey depending on the relative abundance, then the system becomes stable and the feeding switching also enhances the species persistence (Pal et al., 2014). In contrast, Tanabe and Namba (2005) numerically explored that if the consumption rate (omnivory) of the top predator on the basal prey is increased, then the three species Lotka–Volterra model with linear functional responses exhibits chaotic dynamics. They suggested that omnivory destabilizes the system and creates chaos. It is worthy to note that no species exclusion was observed due to increase in omnivory. In the present paper, we will investigate the impact of predator switching in the stability dynamics of the three species Lotka–Volterra model with omnivory (Tanabe and Namba, 2005).

The paper is organized as follows. After discussing some preliminary biological background, we introduce the model in Section 3, and analyze its behavior in Section 4. Control of the chaotic behavior is contained in Section 5, and finally the paper is ended with a brief conclusion.

2. Background

Murdoch (1969) explored that in switching mechanism, the number of attacks upon a species is disproportionately large when the species is abundant relative to another prey, and disproportionately small when the species is relatively rare. Predator feeding switching is an important aspect in nature, (Fisher-Piette, 1934; Holt, 1997). However, the effect of predator switching in an omnivory system, does not appear to be properly investigated yet. In a tri-trophic food chain or food web with omnivory, the top predator consumes both the middle predator and the basal prey. The top predator switches its predation between middle predator and basal prey in the same or another habitat, when the preferred prey declines due to heavy predation.

Experimental results suggest that predator switching is a phenomenon that is very likely to occur with omnivory feeding (Gismervikl et al., 1997). Holt and Polis (1997) have intuitively suggested that if the adaptive foraging by the omnivore predator leads to switching between the prey and the intermediate predator, the system will be stabilized. Our aim is to investigate and substantiate this claim, by providing a theoretical setting for the effect of predator feeding switching in an omnivory system considering a suitable mathematical model.

3. Model

In the three species food chain model proposed by Tanabe and Namba (2005), chaotic behavior is discovered. We want to consider a modification of this model, incorporating top predator feeding switching behavior in it. Let x, y and z respectively denote the prey, middle predator and top predator population sizes. The resulting system of equations reads as follows.

$$\begin{aligned}\frac{dx}{dt} &= (b_1 - a_{11}x)x - a_{12}xy - \frac{a_{13}xz}{1 + c\dfrac{y}{x}},\\ \frac{dy}{dt} &= -b_2 y + a_{21}xy - \frac{a_{23}yz}{1 + c\dfrac{x}{y}},\\ \frac{dz}{dt} &= -b_3 z + \frac{a_{31}xz}{1 + c\dfrac{y}{x}} + \frac{a_{32}yz}{1 + c\dfrac{x}{y}}.\end{aligned} \tag{3.1}$$

As it occurs for the switching models, the system (3.1) is not well defined at the origin. To overcome the occurrence of the singularity there, we simply replace the above equations at (0, 0, 0) by the following ones:

$$\frac{dx}{dt} = \frac{dy}{dt} = \frac{dz}{dt} = 0.$$

The meaning of the parameters, all nonnegative, is as follows. b_1 is the prey intrinsic net growth rate, while a_{11} denotes their intraspecific competition for resources. The parameters a_{ij} with $i < j$ denote the prey consumption rates, while a_{ij} for $i > j$ represent the corresponding predators' assimilation rates. The natural mortalities of the intermediate and top predators are respectively b_2 and b_3.

Therefore, the first equation expresses logistic growth of the prey in the absence of predators. When they are present, the prey is subjected to their hunting. In the absence of prey, the intermediate predator is bound to starve; in the food chain, it also represents a possible source of food for the top predator. The latter feeds on both prey and intermediate predators.

The feature of this model resides in the last terms of the first two equations and the corresponding last two terms of the last equation, modeling the feeding switching behavior between the two types of prey for the top predator, following (Tansky, 1978). This mechanism is governed by the relative abundances of the bottom prey and intermediate predators. The parameter c represents the switching intensity. This parameter provides also a mean to obtain a continuum of models. In fact, note that for $c = 0$ the system shows no switching behavior, it becomes exactly the Tanabe and Namba three species omnivory system, (Tanabe and Namba, 2005), while for $c = 1$ the switching function is the same function defined by Tansky, (Tansky, 1978). This parameter thus allows to control the amount of switching feeding that the top predator can use.

Recently, we have studied the Hastings-Powell (H-P) model by considering omnivory and predator switching in the model system (Pal et al., 2014). We have explored that omnivory may stabilize the chaotic H-P system, however, above a threshold value of omnivory, species exclusion may happen. In that situation, predator switching enhances system stability and prevents species extinction. It is worthy to mention here that the present model (3.1) can be derived from the H-P model with omnivory and predator switching (Pal et al., 2014) if we set $b_1 = b_2 = b_3 = 0$. Comparing the generic case where not all of the three parameters are zero with the special case, the omnivory dynamics are very different. In the absence of predator switching ($c = 0$), we have explored that omnivory may stabilize the chaotic H-P system (Pal et al., 2014), whereas, Tanabe and Namba (2005) have explored that omnivory can create chaos in a three species L–V model. It is already mentioned earlier that predator switching is an important aspect in food web dynamics. To